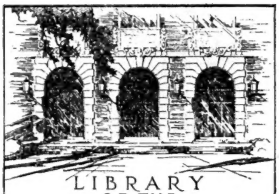

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NOTES ON THE ANATOMY OF THE TREESHREW DENDROGALE

BY D. DWIGHT DAVIS
ASSISTANT CURATOR OF ANATOMY AND OSTEOLOGY

The recent researches of Clark, Gregory, and others have focused a great deal of attention on the morphology of the treeshrews. The fact that the Tupaiidae are now generally recognized as the closest living relatives of the Primates has brought them within the purview of those interested in the evolutionary history of man, so that information regarding them is of more than ordinary interest.

There has been a tendency among many who have worked on the morphology of these animals to lump all treeshrews together in the two genera *Tupaia* and *Ptilocercus*, in spite of the fact that Lyon (1913) in his extensive monograph of the family recognized no less than six genera. Failure of non-systematists to give adequate consideration to the remaining genera is probably due to their rarity and to the fact that all bear a close superficial resemblance to *Tupaia*. The results of the present study illustrate the inadvisability of placing too much faith in external similarity when dealing with survivors of decadent stocks.

The genus *Dendrogale* is one of the rarest of the Tupaiidae. It includes the smallest members of the family. Fully adult individuals may have a body length of only 120 mm. Nothing is known of their habits. The three specimens upon which the present study is based were all shot from trees in broad daylight, and certain features of the anatomy indicate that they are more arboreal than *Tupaia*.

The stomach of the specimen dissected was distended with well-chewed but undigested food. This material was examined by Mr. W. J. Gerhard and Mr. Emil Liljeblad, entomologists of Field Museum. It consisted, apparently exclusively, of fragments of beetles of various types.

The material for this study was collected by Dr. W. H. Osgood in southern Annam, French Indo-China, in March and April, 1937. It consisted of a complete skeleton of an adult male, a formalin-preserved body of a slightly younger, but fully adult, male, and study skins and skulls of a male and female. The individual from which the skeleton was obtained was originally preserved entire in formalin. Unfortunately the jar in which this specimen was shipped was broken during transit and the animal arrived in a completely desiccated condition. All efforts to resoften it having failed, it was reduced to a skeleton. The species represented is *Dendrogale frenata* Gray.

Despite the scanty material, it was decided that the rarity of the genus and the interest that attaches to the treeshrews in general warranted anatomical study. This decision has been more than justified by the unexpectedly interesting nature of the results.

A complete skeleton of *Tupaia belangeri concolor* from Ban Me Thuot, Annam, and a skeleton of *Tana tana utara*, without feet, from Sandakan, British North Borneo, have been available for comparison. Through the courtesy of the authorities of the United States National Museum the following skeletons were also examined: *Tupaia javanica* from Goenseng Boender, Java; *Tupaia n. nicobarica* from Great Nicobar; and *Tana t. tana* (without feet) from Deli, Sumatra. A rather poorly preserved specimen of *Tupaia belangeri modesta* in alcohol was also used for comparison.

The drawings were made by Mr. John J. Janecek from original sketches made by the author.

Especial acknowledgment is due Professor W. E. Le Gros Clark. This study would have been virtually impossible without his painstaking research on other tupaiids. His studies have been constantly consulted, and the form of my presentation has been largely guided by his accurate descriptions.

SKELETON

The skeleton is quite well known in *Tupaia* and *Ptilocercus*. Since the skeleton of *Dendrogale* is essentially similar to that of other tupaiids, detailed description seems unnecessary. The following notes have been restricted to points that are of interest from the comparative standpoint.

Skull.—The skull of *Dendrogale* is quite well known. It was figured and described briefly by Lyon (1913), who pointed out that it is very similar to that of the short-nosed species of *Tupaia*. The

only conspicuous differences are the reduction of the large zygomatic fenestra found in *Tupaia* to a minute foramen in *Dendrogale*, and the absence of palatal fenestrae. Both these characters are shared by *Ptilocercus*.

A supraorbital foramen, which is absent in *Ptilocercus*, is present and well developed in *Dendrogale*.

The brain case is somewhat more rounded, less angular, and shorter antero-posteriorly than it is in *Tupaia*. This is true even in fully adult individuals, a fact that Lyon was unable to determine because of lack of suitable material. A short sagittal crest is developed in old individuals, and the temporal crests are well defined and rounded posteriorly, so that they take the form of a U. The occipital crest is low but well developed.

Dentition.—The dentition differs little from that of *Tupaia*. The upper canine is two-rooted as in *Ptilocercus*, but lacks the small basal cusp. This tooth has a single root in both *Tupaia* and *Tana*. The third upper premolar is two-rooted. The fourth, which may be two-rooted and without any evidence of a protocone in a few species of *Tupaia*, is three-rooted and molariform in *Dendrogale*. The hypocones on the upper molars are reduced as compared with *Tupaia*.

Vertebral Column.—This region shows little of special interest. The vertebral formula is C7, D13, L6, S3, C27. In the cervical region a spinous process is present only on the axis and the seventh vertebra. The eleventh dorsal is the anticlinal. This is the same as Clark found in *Ptilocercus*, and contrasts with the tenth in the three skeletons of *Tupaia* and two of *Tana* examined. The spines on all the dorsals are about as well developed as in *Tupaia*. The lumbars do not differ from those of *Tupaia*, except that the anapophyses and transverse processes are somewhat less prominent. The sacrum is composed of the usual three fused vertebrae. A prominent spine is present on all but the first of these. Only the first segment articulates with the ilium; in this *Dendrogale* agrees with *Tupaia* and contrasts with *Ptilocercus* where the first two sacral segments are in contact with the ilium.

Sternum.—The sternum is not especially peculiar. The presternum is expanded anteriorly, with a rounded cephalic border, and a cylindrical body posteriorly. The mesosternum consists of the customary five segments. The xiphisternum is about twice as long as a mesosternal segment, and ends in a large, rounded cartilage.

Ribs.—These bones are narrow as in *Tupaia*, not broad and flattened as are those of *Ptilocercus*. There are thirteen pairs. Eight pairs articulate directly with the sternum, two indirectly, and three are floating.

Shoulder Girdle and Forelimb.—The clavicle is similar to that of other tupaiids. It is less curved than that of *Tupaia*, but somewhat more so than that of *Tana*.

The scapula is slightly narrower than in other tupaiids. It is more triangular in outline, the cephalic border not being rounded as it is in *Tupaia* and *Tana*. As in other members of this family, there is a distinct tubercle on the ventral border of the acromion for the attachment of the deltoid muscle.

The deltoid crest on the humerus is not nearly so prominent nor so long as it is in other tupaiids. The median epicondyle is much less prominent, but there is a conspicuous entepicondylar foramen. This foramen is absent in the skeleton of *Tupaia belangeri* examined, but is present in the other two species of this genus and in both specimens of *Tana*. The ulna and radius do not present any conspicuous peculiarities.

The carpus is strikingly similar to that of *Ptilocercus*. The scaphoid and lunar are separate, instead of being fused into a single bone as they are in *Tupaia*. Examination of the carpus in a study skin of *Tana tana* shows that these bones are fused, as in *Tupaia*. In keeping with the fused condition of the scaphoid and lunar in *Dendrogale* the magnum articulates with the lunar, rather than with the cuneiform.

Pelvis and Lower Limb.—The pelvis resembles that of *Tupaia* very closely, although it is somewhat more slightly built. The ilia are spatulate. The symphysis is shortened, probably in correlation with arboreal habits, as in *Ptilocercus*. The femoral process in front of the acetabulum is much reduced as compared with *Tupaia* and *Tana*. The pectineal eminence on the pubis is scarcely indicated.

The femur does not differ essentially from that of *Tupaia*. The trochanter and lateral crest are somewhat less prominent, and the head is set at a slightly less acute angle. The lateral crest on the tibia is less developed and its border is more medial in position than it is in *Tupaia*. The fibula is extremely slender and perfectly straight. It is completely separate from the tibia. The tarsus is like that of *Tupaia*, the calcaneum articulating with the cuboid. According to Clark these two bones are completely separated by the astragalus and the navicular in *Ptilocercus*.

MUSCLES

The myology of both *Tupaia* and *Ptilocercus* has been fully described by Clark. Although his descriptions are excellent, the illustrations, particularly those accompanying his paper on *Tupaia*, leave much to be desired. For this reason the myology in *Dendrogale* has been figured in some detail.

Unfortunately the muscles of the head, the lower limbs, and most of the neck were destroyed before the specimen was preserved. The rest of the body was in excellent condition, however, permitting a very thorough dissection.

The arrangement of the muscles is, in general, similar to that of *Tupaia*, and in the present study comparisons have constantly been drawn with Clark's description of the muscular anatomy of that animal.

MUSCLES OF THE THORAX
(Figures 49, 50, 52)

M. pectoralis major is very similar to the same muscle in *Tupaia*. It is slightly overlapped posteriorly by the pectoralis abdominis and the transversus abdominis, as noted by Clark in *Tupaia*. There is no attachment to the clavicle. It inserts into the bicipital groove of the humerus. The branch of the median anterior thoracic nerve supplying it passes between the pectoralis minor and the pectoralis abdominis, and not partly through the pectoralis minor as Clark found in *Tupaia*.

M. pectoralis minor originates from the sternal ends of the fourth to sixth sternal cartilages. No origin from the third, which Clark found in *Tupaia*, was found. It inserts into the capsule of the shoulder joint, beneath the deltoideus.

M. pectoralis abdominis (abdomino-humeralis of Clark) forms a median raphe with its fellow from the opposite side at a point just ventrad of the xiphisternum. The fibers converge and insert, partly beneath but mostly lateral to, the insertion of the pectoralis minor on the shoulder capsule.

M. subclavius is a small but well-marked muscle. It originates from the sternal end of the anterior surface of the first costal cartilage. There is no attachment to the rib itself, as Clark found in *Tupaia*. The muscle extends obliquely forward and outward to insert on the posterior and inferior surfaces of the distal half of the clavicle. None of the fibers reach the coraco-clavicular ligament.

M. serratus anticus originates from the transverse processes of the last four cervical vertebrae and the first eight ribs. The last

four slips interdigitate with the obliquus abdominis. The next one forward emerges between the scalenus anterior and intermedius. A few of the most ventral fibers of the scalenus anticus pass external to it, instead of internal. The remaining anterior part of the muscle emerges from beneath the scalenus anticus.

As in *Tupaia*, insertion takes place on the vertebral border of the scapula. The fibers from the last four digitations converge to insert on the inferior angle.

M. levator scapulae originates from the axis near its ventral midline. Passing backward as a narrow band, its dorsal border becomes almost inseparably bound to the ventral border of the trapezius. It inserts on the coracoid process of the scapula as a direct continuation of the insertion of the trapezius.

M. sternocostalis is narrow and poorly developed. It originates from the ventral surface of the first costal cartilage, between the origins of the scalenus posterior and the rectus abdominis. About halfway back it thins out into an exceedingly thin aponeurosis which inserts on the fifth costal cartilage near its sternal end.

MUSCLES OF THE SHOULDER GIRDLE AND UPPER ARM
(Figures 49–52)

M. trapezius.—The anterior limits of the origin of the acromial part of this muscle could not be determined because of the condition of the specimen. The remainder of the origin does not differ from that of *Tupaia*. It extends along the midline as far back as the second thoracic vertebra. The origin of the spinous part extends from here to the first lumbar vertebra. The two divisions meet in a raphe over the scapular spine.

The acromial division inserts along the upper border of the scapular spine, from the metacromion to its dorsal tip. The spinous part inserts on the dorsal third of the lower border of the spine.

M. latissimus dorsi originates from the dorsal midline, beginning just posterior to the spine of the scapula and extending back to a point a few millimeters in front of the iliac crest. In the lumbar region the muscle proper does not reach the midline, but is continued toward it as a thin aponeurosis. As in *Tupaia*, there is no attachment to the iliac crest or to the lower ribs. It is inserted into the bicipital groove.

M. supraspinatus arises from the supraspinous fossa and spine of the scapula. The muscle is partly divisible into two bellies.

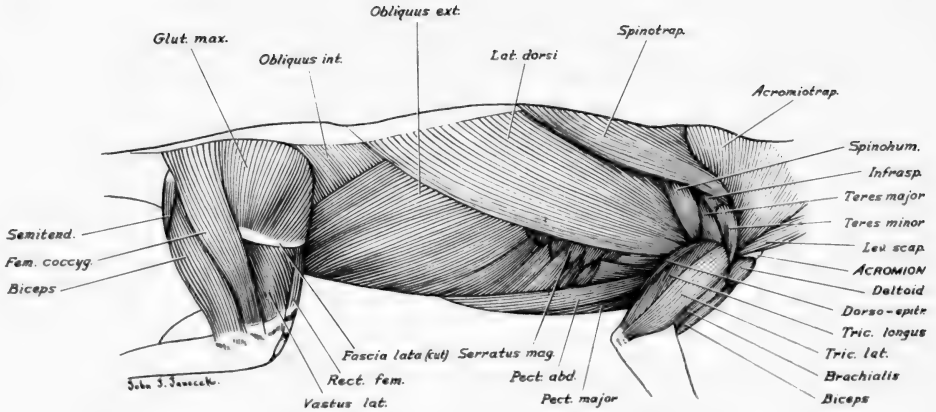

FIG. 49. Superficial body musculature from the right side. ×1½.

The more superficial arises from the dorsal surface of the scapular spine, the deeper belly from the supraspinous fossa. Both pass under the acromion process to insert tendinously on the greater tuberosity of the humerus.

M. infraspinatus originates from the infraspinous fossa. Its lower half is concealed by the teres minor. It inserts by a stout tendon on the head of the humerus, immediately behind the insertion of the supraspinatus.

M. deltoideus arises from the anterior edge of the distal half of the clavicle and tendinously from the ventral edge of the acromion process. The acromial origin is much less extensive than that figured by Clark for *Tupaia*, and is confined to a small tubercle on the ventral border of the acromion. The fibers from these two origins converge, giving a bipinnate form to the muscle, and insert on the deltoid crest of the humerus. As in *Tupaia* the spinal division of this muscle is absent.

M. teres major originates from the inferior angle and most of the length of the axillary border of the scapula, and dorsally from the fascia covering the infraspinatus. It inserts by a wide, flat tendon into the lesser tuberosity of the humerus, beneath and immediately posterior to the insertion of the latissimus dorsi.

M. teres minor originates aponeurotically from the fascia of the infraspinatus. A very few of the fibers may arise from the medial part of the scapular spine. It inserts tendinously on the humerus close to the insertion of the infraspinatus.

Clark states that the teres minor conceals the infraspinatus completely in *Tupaia*. In *Dendrogale*, however, it does not extend beyond the center of the scapula, so that much of the vertebral end of the infraspinatus is not hidden.

M. spinohumeralis.—Clark describes this muscle in *Tupaia*, but does not mention it in connection with *Ptilocercus*. Its relations in *Dendrogale* are much the same as in *Tupaia*.

M. subscapularis is a thick muscle originating from the subscapular fossa. It is divided by four well-marked tendinous intersections. The fibers converge, to insert tendinously on the lesser tuberosity of the humerus, beneath and immediately behind the insertion of the supraspinatus.

M. biceps arises by a long, stout tendon from the supraglenoid tubercle. There is no short (coracoid) head, which Clark found in both *Tupaia* and *Ptilocercus*. It inserts by a stout tendon into the radial tubercle.

M. coracobrachialis originates from the tip of the coracoid process. As in *Tupaia* it is composed of two heads. The very small short head originates non-tendinously beneath the origin of the long head. It passes downward across the neck of the humerus to insert

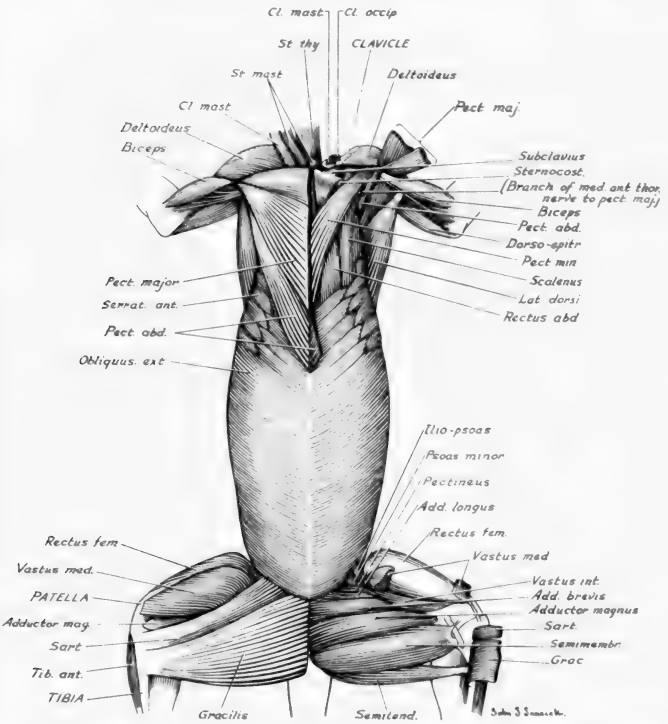

FIG. 50. Ventral body musculature. Superficial layer on the left, deeper muscles on the right. ×1.

on the inner lip of the bicipital groove, behind and mostly above the insertion of the teres major. The long head originates tendinously. Part of the fibers insert on the medial side of the shaft of the humerus, immediately below the insertion of the latissimus dorsi. The tendon, which runs the entire length of the muscle, continues beyond this insertion to connect with a muscular insertion on the

median epicondyle and for a short distance on the shaft of the humerus above it.

M. brachialis anticus is separable into medial and lateral heads, as in *Tupaia*. The medial head arises from the anterior surface of the shaft of the humerus below the deltoid crest. The lateral head originates from the outer side of the shaft, from the level of the

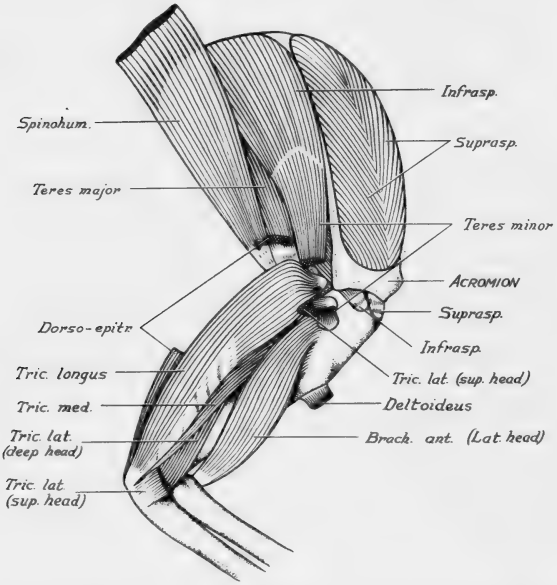

FIG. 51. Musculature of the shoulder and upper arm, lateral aspect. In several of the muscles a section has been removed from the center in order to expose underlying structures. ×3.

distal end of the deltoid crest up to the insertion of the teres minor. The two heads unite and insert by a single tendon into the coronoid process of the ulna.

M. dorso-epitrochlearis, as in *Tupaia*, is composed of two heads. One originates from the latissimus dorsi, while the other takes origin in a similar way from the teres major, a few of the fibers originating from the spinohumeralis. The two heads embrace the spinohumeralis between them. The separate insertion of these two heads on the

olecranon which Clark describes in *Tupaia* is not found in *Dendrogale*. The two heads fuse into a single mass which inserts by a rather fine tendon on the medial side of the distal end of the olecranon.

M. triceps lateralis is composed of a superficial and a deep head, as in *Tupaia*. The superficial head is a large muscular mass which originates by a rather small tendon from the greater tuberosity of

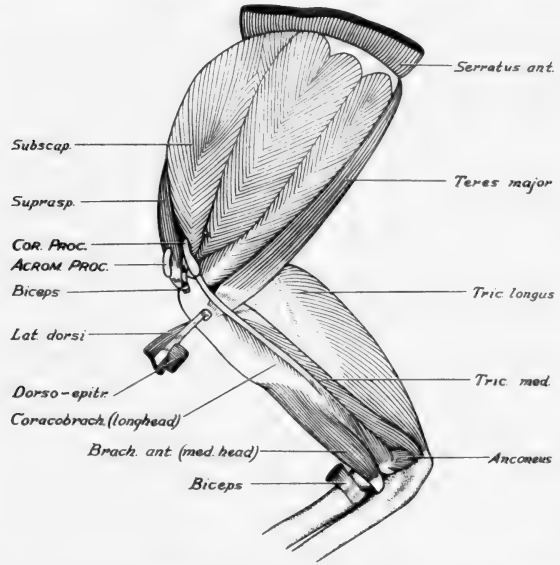

FIG. 52. Musculature of the shoulder and upper arm, medial aspect. The latissimus dorsi has been reflected to the left, and most of the dorso-epitrochlearis and biceps have been removed. ×3.

the humerus. Its origin is beneath the teres major, and immediately above and behind the insertion of that muscle. The deep head is very small, originating on the distal half of the shaft of the humerus.

As in *Tupaia*, the main mass of the muscle inserts on the proximal end of the olecranon, while an aponeurotic expansion of the superficial part inserts on the lateral border of the olecranon.

M. triceps longus originates by a short, stout tendon from the infraglenoid tubercle and inserts on the posterior end of the ole-

cranon. It inserts tendinously on the extreme distal end of the olecranon.

M. triceps medialis is apparently somewhat better developed in *Dendrogale* than in *Tupaia*. It originates from the medial surface of the shaft of the humerus as far up as the head, and inserts into the proximal end of the olecranon.

M. anconeus is well developed and quite distinct from the triceps medialis, contrary to what Clark found in *Tupaia* and *Ptilocercus*. It originates on the median epicondyle and inserts on the proximal end of the olecranon, hard by the insertion of the triceps medialis.

MUSCLES OF THE HIP
(Figures 49, 50)

M. psoas minor.—The origin of this muscle is completely separate from that of the psoas major. It arises from the first three lumbar vertebrae. Just behind the third lumbar it becomes a wide, flat tendon, which inserts on the crest of the pubis, close to the symphysis.

M. psoas major arises from the lumbar vertebrae, from the third to the sixth inclusive, and from the anterior part of the body of the sacrum. It lies completely dorsal to the psoas minor. Insertion is made on the lesser trochanter of the femur, immediately proximal to the insertion of the iliacus.

M. iliacus is quite similar to the corresponding muscle in *Tupaia*. It consists of the usual lateral and medial heads. The powerful lateral head originates from the quadratus lumborum, although it overlies that muscle broadly. The medial head is much less powerfully developed, in contrast with what Clark found in *Ptilocercus*. It arises from the iliac fossa and inserts, together with the lateral head, on the lesser trochanter.

M. quadratus lumborum is much narrower than the iliacus, whose wide lateral head hides it completely from the ventral side. It arises by a tendon, considerably narrower than the tendon on the psoas minor and almost hidden by muscle fibers, from the iliac crest. There are adventitious origins from the tips of the transverse processes of all the lumbar vertebrae. Insertion is made into the transverse processes and sides of the bodies of the lumbar and last four thoracic vertebrae.

M. sartorius arises from the central part of the inguinal ligament, as in *Ptilocercus*. None of the fibers reach the pubic spine. It inserts on the anteromedial surface of the tibia, immediately proximal to the insertion of the gracilis.

M. gluteus maximus arises from the whole anterior edge of the iliac crest and from the lumbo-dorsal crest as far back as the end of the sacrum. There is no origin from the sacral spines, which Clark found in *Tupaia*. As in *Tupaia* the anterior fibers insert on the fascia lata, and there is even an incipient separation between this part of the muscle and the posterior part. The fibers from the posterior part converge and insert tendinously on the third trochanter of the femur. They are partly overlapped by the anterior edge of the femorococcygeus.

Mm. gluteus medius and *minimus* do not differ greatly from the same muscles in *Tupaia*. They are quite readily separable, contrary to what Clark found in *Tupaia*. The medius is bilaminar. It arises from the lateral surface of the dorsum ilii. As in *Ptilocercus* the superficial fibers insert below those of the deeper division, which inserts on the lateral aspects of the great trochanter. The minimus originates along the ventral border of the dorsum ilii and inserts tendinously on the anterior surface of the great trochanter.

M. gemellus is very similar to the corresponding muscle in *Tupaia*. It originates from the margin of the sciatic notch and extends forward to insert on the posterior surface of the great trochanter together with the obturator internus. As in *Tupaia* it is a single muscle.

M. piriformis does not differ from the corresponding muscle in *Tupaia*.

Mm. obturatores are likewise like those of *Tupaia*.

M. quadratus femoris is a thin, triangular muscle layer which originates on the pubic arch in front of and deep to the semimembranosus. It inserts into the posterior surface of the shaft of the femur.

M. femorococcygeus is wholly separable from the gluteus maximus, its anterior edge overlapping that muscle from the origin down to the insertion of the gluteus. It arises from the transverse processes of the first three caudal vertebrae and extends the length of the thigh, inserting into the thigh by a series of fleshy digitations from a point immediately below the insertion of the gluteus maximus down to the lateral surface of the lateral condyle, into the tendon of the gastrocnemius, and into the fabella. The condition of this muscle is very similar to that described by Clark for *Ptilocercus*.

MUSCLES OF THE THIGH
(Figures 49, 50)

M. semimembranosus arises, partly tendinously and partly by fleshy fibers, from the ischial tuberosity immediately below the

origin of the biceps and from the posterior border of the ischium almost as far forward as the symphysis. This exceedingly powerful muscle inserts on the medial surface of the medial tibial condyle just below the articulating surface and behind the internal lateral ligament. A second much weaker tendon passes over the ligament to insert on the condyle of the femur. This insertion is almost identical with what Clark found in *Tupaia*, and differs considerably from that of *Ptilocercus*.

M. semitendinosus originates by two heads, as in both *Tupaia* and *Ptilocercus*. One is from the second and third caudal vertebrae, beneath the femorococcygealis, and the other from the ischial tuberosity deep to the origin of the biceps. The two heads fuse a short distance below their origin and extend across the thigh as a single muscle. Insertion is made by a wide, flat tendon on the crest of the tibia, immediately beneath the insertion of the gracilis.

M. biceps femoris arises by a tendon from the ischial tuberosity. This muscle inserts by a wide fascial expansion into the outer surface of the leg. This fascial expansion runs forward to the tibial crest, and is a direct continuation of the fascia of the femorococcygealis. None of the fibers reach the fibula.

M. tenuissimus originates from the fascia covering the dorsal caudal musculature, immediately behind the posterior edge of the gluteus maximus and beneath the femorococcygealis. In the specimen dissected the tenuissimus does not reach the lower leg on either side of the body, but is inserted aponeurotically into the inner face of the biceps, near its posterior border.

M. rectus femoris arises by a single exceedingly stout and rather wide tendon from the anterior inferior iliac spine only. There is no origin from the margin of the acetabulum, and in this respect *Dendrogale* differs from both *Tupaia* and *Ptilocercus*. It inserts by a powerful tendon into the upper border of the patella.

M. vastus lateralis originates on the anterior aspect of the great trochanter immediately below the insertion of the gluteus minimus, as in *Tupaia*. The fibers of this large muscle converge and insert, partly aponeurotically along the tendinous part of the rectus femoris, partly aponeurotically on the lateral edge of the patella, and partly on the quadriceps tendon.

M. vastus intermedius originates from the anterior, medial, and lateral faces of the shaft of the femur for more than half its proximal length. It inserts by a stout tendon into the upper margin of the patella.

M. vastus medialis.—The origin of this well-developed muscle extends along the anterior face of the upper quarter of the shaft of the femur to a point on the anterior face of the great trochanter deep to the origin of the vastus lateralis. It inserts into the medial side of the quadriceps tendon and aponeurotically into the medial border of the patella.

M. pectineus is a short, heavy muscle. It originates from the front of the pubis, immediately lateral to the symphysis, and inserts tendinously into the shaft of the femur immediately proximal to the insertion of the adductor longus.

M. gracilis is a very broad, thin sheet of muscle. It originates from the extreme medial end of the inguinal ligament and from the whole length of the pubic arch to one side of the symphysis. It inserts on the antero-mesial surface of the tibia, just distal to the insertion of the sartorius.

M. adductor magnus originates from the central part of the pubic ramus, from a point just in front of the origin of the semimembranosus forward about halfway along the symphysial border. As in both *Tupaia* and *Ptilocercus*, there is no attachment to the tuber ischii. It inserts on the posterior face of the femur, from the third trochanter down to the popliteal region.

M. adductor brevis does not differ from the corresponding muscle in *Tupaia*. It originates from the central part of the pubic arch, lateral to the symphysis, and inserts into the posterior surface of the shaft of the femur from the lower edge of the pectineus "to the junction of the third and lower quarters of the femur."

M. adductor longus arises from the anterior end of the pubic arch between the origins of the adductor brevis and the pectineus. It inserts into the middle of the shaft of the femur. There is no aponeurotic expansion at its insertion, as Clark described for *Tupaia*.

RESPIRATORY SYSTEM

Larynx.—This structure (fig. 53) differs in several details from the larynx in *Ptilocercus*. There is no prominence on the thyroid cartilage for the attachment of the sternothyroid and thyrohyoid muscles. The foramen for the exit of the internal laryngeal nerve is located only one-quarter of the distance from the lateral border to the midline of this cartilage, and it is approximately midway between the anterior and posterior borders. A short superior cornu is present.

The epiglottis and cricoid and arytenoid cartilages do not differ essentially from those described and figured by Clark for *Ptilocercus*.

The epiglottis is considerably larger, and the muscular processes on the arytenoid cartilages are less prominent.

Trachea and Lungs.—The trachea is composed of 20 incomplete cartilaginous rings. The division into bronchi is similar to that of *Ptilocercus*. The division and relation of the parts of the lungs are also similar.

DIGESTIVE SYSTEM

All parts of the digestive system anterior to the pharynx were removed with the head.

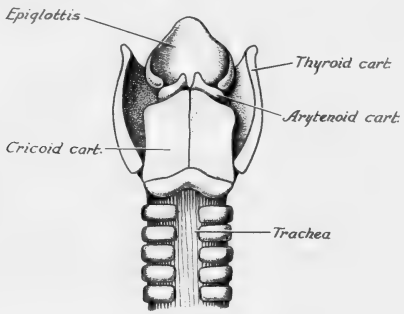

FIG. 53. Dorsal aspect of the larynx. ×6.

The *Oesophagus* is a straight, simple tube about 32 mm. long.

The *Stomach* (fig. 54, *a*) is purse-shaped, its vertical diameter exceeding its transverse diameter only slightly. In this respect it differs rather widely from that of either *Tupaia* or *Ptilocercus*. In general outline the stomach approaches that of *Tupaia*, but in the development of the fundus and in the presence of a sulcus intermedius it resembles that of *Ptilocercus*.

The stomach wall is quite thin in the region of the fundus. It becomes considerably thicker in the cardiac and pyloric regions, due chiefly to the greatly increased thickness of the mucous layer at these points.

Internally the mucous lining is thrown up into a series of very prominent longitudinal ridges. These are wholly absent in the fundus, are only moderately developed in the pyloric end, and are most prominent in the cardiac region, where the mucous layer greatly exceeds the muscular layer in thickness.

The *Small Intestine* measures approximately 140 mm. in length. As in *Ptilocercus*, the coils are not arranged in any definite order. There is a rotation of the terminal part of this structure (fig. 54, *b*) similar to that described and figured by Clark for *Ptilocercus*.

The *Colon* is a straight, simple tube, not exceeding the small intestine in diameter. It is approximately 27 mm. long (the anus was removed with the skin). The ileo-colic junction is marked by a faint constriction.

There is a well-developed *Caecum* (fig. 54, *b*) at the anterior end of the colon. The neck is narrow, but the body of the structure is expanded to about the diameter of the colon. In its normal position

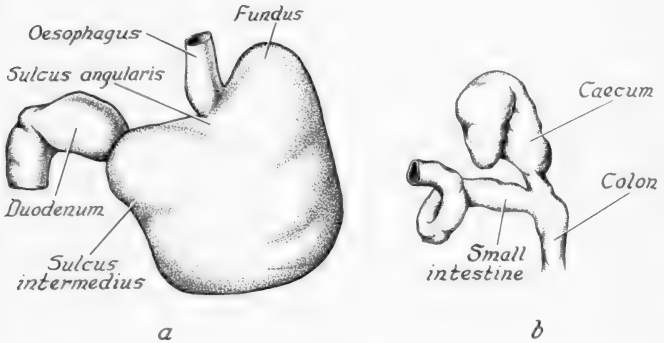

FIG. 54. *a*. The stomach, seen from the side. *b*. Junction of the small and large intestines. The caecum has been reflected upward. ×2.

the structure is reflected ventrally and caudally over the colon, and its distal end is bent to the left upon itself.

The *Liver* (fig. 55) is in general similar to that of *Ptilocercus*, but differs in a number of details. It has a breadth of 20 mm. and a dorso-ventral diameter of 14 mm., thus differing considerably from that of *Ptilocercus*, where these proportions are reversed. It is divided into the usual three main lobes, the right lateral, central, and left lateral, of which the central and left lateral are nearly of equal size and the right lateral the smallest. There is no division of the central lobe into right and left lobules except by the line of the suspensory ligament, and this lobe forms scarcely more than half of the diaphragmatic surface of the liver. The cardiac notch is very shallow in contrast with the deep one found in *Ptilocercus*.

The fossa for the gall bladder is situated at the juncture of the central and right lateral lobes, but most of the organ lies in a notch in the central lobe. The caudate lobe on the posterior surface of the right lateral lobe is larger than in *Ptilocercus*, and more dorsal in position. The two processes on the right lobe which Clark homologizes with the Spigelian lobe differ considerably from the condition in *Ptilocercus*. They are separated from the caudate lobe by a thin

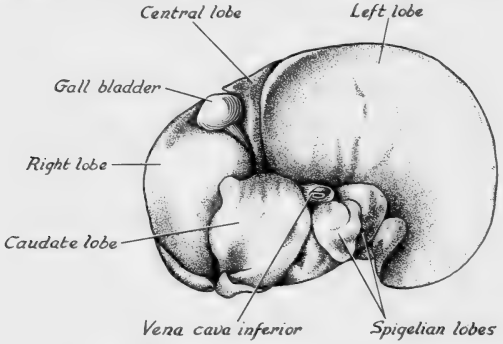

FIG. 55. Posterior surface of the liver. ×3.

layer of the substance of the right lobe. The venous lobe is small and rounded and projects caudally dorsal to the vena cava. The papillary process resembles that of *Ptilocercus*, but is considerably larger.

The *Gall Bladder* and its ducts are similar to those of *Ptilocercus*.

The *Pancreas* is a large, irregularly shaped gland lying dorsal to the stomach. The pars duodenalis is narrow. The superior mesenteric vessels run through a deep notch in its cephalic border, instead of piercing the gland as in *Ptilocercus*. The omental lobe is very small. The pars linealis is narrow.

The *Spleen* is long and narrow. It lies in front and to the left of the pancreas, above the cardiac end of the stomach. It is divided into a series of irregular lobules by deep transverse fissures. The anterior end of the organ bends abruptly toward the midline, giving the whole structure the form of an inverted and reversed J.

MALE UROGENITAL SYSTEM
(Figure 57)

The scrotum, testicles, and part of the penis were removed in skinning. The remainder of the urogenital system is well preserved,

however, and supplies much interesting information when comparison is made with the corresponding structures in *Tupaia* and *Ptilocercus*.

The *Kidneys* apparently are very similar to those of *Ptilocercus*. The right is not situated higher than the left, however, as Clark found to be the case in *Ptilocercus*. Each organ measures about 11 mm. long by 7 mm. wide. The anterior pole is broader than the posterior.

The *Prostate* encircles the proximal end of the urethra, immediately below the mouth of the bladder. Superficially it appears to be very similar to the corresponding organ in *Ptilocercus*, and to differ considerably from the prostate in *Tupaia*.

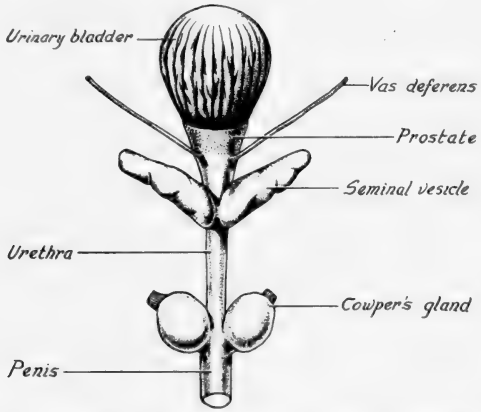

FIG. 56. Proximal part of the male urogenital system, dorsal aspect. ×3.

The *Vasa Deferentia* enter the urethra immediately below the prostate and some distance above the seminal vesicles. This contrasts sharply with the intimate relation that Clark found to exist between the vasa and the vesicles in *Ptilocercus*.

The *Seminal Vesicles* agree quite closely with those of *Ptilocercus*. Each is an elongate, slightly lobulated structure. A constriction near the center of each organ probably marks the division between the vesicular gland and the vesicular diverticulum which Clark distinguished in *Ptilocercus*.

The absence of a *Uterus Masculinus* is noteworthy, as this structure is present and well developed in both *Tupaia* and *Ptilocercus*.

The *Cowper's Glands* are a pair of ovate, smooth-walled bodies lying on either side of the urethra immediately behind the crus penis. They open into the urethra by very short ducts.

Only the proximal half of the *Penis* is present, its tip having been removed with the skin. It is a rather stout structure, firmly attached to the ischio-pubic arch by well-developed Mm. ischiocavernosi. The M. levator penis attaches tendinously to its ventral midline.

The *Suprarenals* are somewhat larger than those of *Ptilocercus*. Each measures about 4.5 mm. in length. As in *Ptilocercus*, they are bright yellow, ovate bodies lying against the kidneys, immediately above their hila.

DISCUSSION

It has generally been assumed that *Ptilocercus* occupies a rather isolated position in the family Tupaiidae. This supposed isolation is expressed by the usual practice of placing *Ptilocercus* alone in the subfamily Ptilocercinae. This monogeneric subfamily is equivalent in rank to the Tupaiinae, which contains all the remaining genera of tupaiids.

The postcranial anatomy of *Dendrogale* shows that the great superficial resemblance which this genus bears to *Tupaia* is misleading. Not only does *Dendrogale* differ considerably from *Tupaia* in fundamental anatomical characters, but it is noteworthy that most of the differences are in the direction of *Ptilocercus*. *Dendrogale*, in other words, tends to bridge the gap that has been supposed to exist between *Ptilocercus* and other tupaiids, and to occupy a position somewhere between the two subfamilies. The characters on which this opinion is based may be summarized briefly as follows:

The small size of *Dendrogale* is probably a primitive character.

Superficially the skull is very similar to that of *Tupaia*. It is more primitive, however, in retaining the minute zygomatic fenestra and in the absence of palatal fenestrae. *Dendrogale* shares both these characters with *Ptilocercus*.

The dentition is somewhat less specialized, chiefly in the presence of two roots on the canine and in the slight reduction of the molar hypocones.

The anticlinal vertebra is the eleventh as in *Ptilocercus*, instead of the tenth as in *Tupaia* and *Tana*.

The ribs resemble those of *Tupaia*, but the expanded condition of these bones in *Ptilocercus* is doubtless a secondary acquisition.

The sacro-iliac union agrees with *Tupaia* and differs from *Ptilocercus*.

Dendrogale differs from both *Ptilocercus* and *Tupaia* in the reduction of the median epicondyle on the humerus. This condition probably represents a secondary specialization.

The scaphoid and lunar are not fused. A similar condition obtains in *Ptilocercus*.

The shortened symphysis, a character which is shared by *Ptilocercus*, may be a secondary adaptation to arboreal life.

The M. brachioradialis, which is absent in *Ptilocercus*, is present in *Dendrogale*. Clark's suggestion that its absence is a primitive feature is doubtful.

The absence of the short head of M. biceps is a primitive feature not shared with either *Tupaia* or *Ptilocercus*.

The Mm. gluteus medius and femorococcygeus resemble those of *Ptilocercus* rather than those of *Tupaia*.

The M. semimembranosus is like that of *Tupaia*, and differs from that of *Ptilocercus*.

The condition of the M. tenuissimus seems to be one of secondary degeneration, although its absence is primitive.

The form of the stomach is about midway between that of *Ptilocercus* and that of *Tupaia*.

The liver is closer to that of *Ptilocercus* in the relative size of its lobes, but the position of the gall bladder is as in *Tupaia*. The relation of the gall bladder with reference to the liver lobes as found in *Ptilocercus* is apparently the more primitive.

The colon, which Clark describes as "almost reptilian" in *Ptilocercus*, is even less differentiated in *Dendrogale*.

The urogenital system is strikingly similar to that of *Ptilocercus*, and correspondingly different from that of *Tupaia*. The complete absence of a uterus masculinus is a curious condition which is not easy to interpret, since it is present and well developed in both *Tupaia* and *Ptilocercus*. The separation of the outlets of the vas deferens and the seminal vesicles is also noteworthy. In general, the urogenital system seems to be somewhat less specialized than that of *Ptilocercus*.

Clark, as a result of his researches on *Tupaia* and *Ptilocercus*, concluded that *Ptilocercus* is the most primitive of the treeshrews.

Tupaia, although showing many specializations of its own, would then stand somewhere between *Ptilocercus* and the lemurs in the evolution of the Primates. This view has not been challenged, and is doubtless essentially correct. *Dendrogale*, however, shares many of the primitive characters of *Ptilocercus*, without having acquired its secondary specializations. The available evidence indicates, therefore, that *Dendrogale* may be more primitive than either *Ptilocercus* or *Tupaia*, and perhaps should occupy a place at the bottom of the Primate ladder as far as living survivors of the stock are concerned. These views, of course, may be modified when the anatomy of the remaining tupaiid genera becomes known.

Lyon (1913, p. 36) concluded from a study of skins and skulls of the tupaiids that *Tupaia* "is the most generalized member of the Tupaiidae. . . . It is easy to see how the other members of the family with the exception of *Ptilocercus* have been derived by relatively slight modifications from *Tupaia*." This opinion derives no support from the present study. *Tupaia*, in spite of the great speciation it has undergone and its wide geographic distribution, is more highly specialized than either *Dendrogale* or *Ptilocercus*.

It is obvious that the subfamily Ptilocercinae of Lyon can no longer be recognized, since the family Tupaiidae cannot now be logically broken down into subfamilies.

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